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AN INTERSECTIONAL HYBRID IN HEMIZONIA (COMPOSITAE: MADIINAE)

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The tarweed genus *Hemizonia* consists of 25 annual and six perennial species that bloom in late spring, summer, and fall. They occur throughout the Coast Ranges and valleys of California, northern Baja California, and the adjacent offshore islands. Two of the annual species found in the Southern Coast Ranges are *Hemizonia australis* (Keck) Keck (sect. *Centromadia*, $n = 11$) and *H. ramosissima* Benth. (sect. *'Deinandron' sensu* Keck, $n = 12$). [Apparently Keck (1935, 1958, 1959) did not formally establish this section; it will probably be designated as sect. *Hartmannia* (Gray) Gray (1874, 1876; Tanowitz, ined.)]. Distributions of these two species overlap in the low-lying coastal regions of Santa Barbara County where six intersectional hybrids were discovered. This hybrid combination is apparently rare.

Intersectional hybrids have been described in a number of genera such as *Ceanothus* (Nobs, 1963; Hannan, 1974), *Crepis* (Babcock and Stebbins, 1938), *Ribes* (Keep, 1962), *Helianthus* (Heiser et al., 1962), and *Perityle* (Powell, 1970). A number of intersectional hybrid attempts in *Hemizonia* were made by Clausen (1951). All were highly sterile except for a quite fertile one between *H. pungens* (H. & A.) T. & G. (sect. *Centromadia*, $n = 9$) and *H. ramosissima. Hemizonia pungens,* although well differentiated from other members of its section, clearly belongs in sect. *Centromadia* (Kyhos, pers. comm.). Hybrids at this taxonomic level, however, are rare in nature and can be produced experimentally only with difficulty (Grant, 1963, 1970). It was interesting then to carry out morphological and cytological studies to aid in determining possible phylogenetic relationships between the sections.

Table 1. Morphological Comparison of Hemizonia australis, H. ramosissima, and Putative Hybrids.

Character	*H. australis*	Hybrids	*H. ramosissima*
Shape of leaf tip	apiculate	acute-obtuse	obtuse
Peduncle length:			
maximum (mm)	9.0(3.8–15.0)	10.7(6.0–16.8)	12.5(6.5–22.0)
minimum (mm)	0.0	2.9(0.5– 6.5)	4.0(0.5–12.5)
max/min	0.0	[a]5.3(1.4–13.5)	4.0(1.7–16.0)
Number of heads on ultimate branches	4.9(3–8)	8.7(5–13)	10.4(7–18)
Shape of phyllary tip	apiculate	acute-obtuse	obtuse
Phyllary:			
length (mm)	4.3(3.5–5.5)	[a]4.9(3.5–6.2)	4.2(3.5–5.5)
width (mm)	5.9(5.0–6.5)	4.5(3.0–6.0)	3.1(2.2–4.5)
l/w	0.7(0.5–0.8)	1.1(0.8–1.4)	1.5(0.7–1.9)
Number of ray flowers/head	19(16–22)	8.9(8–10)	5
Number of disc flowers/head	40(33–48)	13.6(9–16)	6
Receptacular bract:			
length (mm)	4.6(4.2–5.0)	[a]5.3(4.5–5.8)	4.9(4.0–6.2)
width (mm)	1.0(0.9–1.1)	[a]1.6(1.5–2.0)	1.4(1.2–1.8)
l/w	2.2(2.0–2.4)	0.4(0.3–0.5)	0.3(0.2–0.4)
Ray corolla:			
length (mm)	5.1(4.5–6.0)	[a]5.5(4.5–6.0)	5.2(3.0–7.0)
width (mm)	1.6(1.2–2.0)	2.2(1.5–2.8)	3.6(3.0–5.0)
l/w	3.2(3.0–4.0)	2.2(2.0–3.5)	1.5(1.0–1.8)
lobe number	2	2 or 3	3
Ray achene:			
length (mm)	1.9(1.5–2.5)	[a]2.2(2.0–2.5)	2.0(1.8–2.5)
width (mm)	1.1(1.0–1.2)	1.0(0.8–1.2)	1.1(1.0–1.5)
l/w	1.6(1.4–1.8)	[a]2.2(1.8–2.7)	1.9(1.2–2.2)
Disc achene length (mm)	1.2(1.5–2.5)	1.4(1.2–1.8)	1.9(1.5–2.5)
Number of pappus paleae/ disc flower	3(3–4)	6(5–7)	7.6(7–10)
Length of pappus paleae/ disc flower:			
maximum (mm)	2.9(2.2–3.0)	2.4(1.8–3.0)	1.4(1.0–1.8)
minimum (mm)	2.6(2.0–3.2)	1.2(1.0–1.5)	1.1(1.0–1.5)
max/min	1.1(1.0–1.2)	[a]2.0(1.3–2.7)	1.3(1.0–1.5)

[a] Numerical values represent the mean of 10 measurements on each of 5 individuals from 20 populations for each of the parents and 20 measurements on each of the 6 hybrids. Note that for some characters the hybrids exceed either of the parental types.

MATERIALS AND METHODS

Comparisons of hybrids and parental taxa for 26 characters are given in Table 1. These were selected for ease of measurement and represent some of the most striking differences in character states. Vouchers of specimens from populations used in this study are listed in Table 2 and are deposited at UCSB.

Meiotic figures in PMC's were obtained from flower buds fixed in a solution of either Newcomer's fixative or modified Carnoy's (ethanol: chloroform:acetic acid, 6:3:2, v/v). Buds were transferred to 70% ethanol for storage. Cells were stained in iron acetocarmine and slides were made permanent following Beeks' method (1955). Pollen was stained in 1% aniline blue in lactophenol for at least 24 hr. Five hundred pollen grains for 20 specimens of *H. australis* and 20 specimens of *H. ramosissima* were scored. Twenty flower buds were sampled from each of the six putative hybrids. Pollen grains that stained evenly were considered viable; unstained or unevenly stained grains were considered inviable.

RESULTS

Meiosis in the parents. Hemizonia australis ($2n = 22$; Venkatesh, 1956; Table 2) exhibits regular meiosis with 11 pairs of morphologically similar chromosomes. There are normally 2 chiasmata per bivalent, one in each arm. There is occasionally an interstitial chiasma formed in one of the arms. This species showed an average of 94.6% stainable pollen, ranging from 86.0 to 99.8% for all populations. *Hemizonia ramosissima* ($2n = 24$; Johansen, 1936; Table 2) also exhibits regular meiotic divisions with 12 bivalents. These chromosomes are morphologically similar as well. The chiasma frequency is approximately two per bivalent with one chiasma per arm. This species showed 98.2% stainable pollen, ranging from 93.6 to 100% for all populations.

Meiosis in the hybrids. Pachytene chromosomes were normally unanalyzable. Late diakinesis and metaphase cells were analyzed in four of the six hybrid plants. Configurations ranged from univalents to hexavalents. Most cells, however, contained only univalents, bivalents, and trivalents (Table 3 and Fig. 1). Bivalents were generally rod-shaped, while trivalents were predominantly forked (Figs. 1,4). Bivalents and trivalents were generally oriented on the equator; univalents were scattered through the cell (Fig. 2). Diakinesis and metaphase cells were often difficult to analyze thoroughly due to the large number of chromosomes, the tendency for the chromosomes to be "sticky", and the reduced pairing. Numbers of other cells were observed in which the complete complement could not be clearly discerned; many of these cells seemingly contained univalents, bivalents, and occasionally a trivalent.

TABLE 2. CHROMOSOME NUMBERS OF HEMIZONIA AUSTRALIS, H. RAMOSISSIMA, AND HYBRIDS USED FOR ANALYSIS IN THIS STUDY. All collections are from Santa Barbara County, California. Collection numbers without name refer to Tanowitz collections.

H. australis (Keck) Keck; $n = 11$.

Field S of Storke and Hollister Rds, *899–1B, 899–R, 1573–A, 1573–B, 1573–L;* field E of Los Carneros and El Colegio Rds, *1576–A, 1576–B, 1576–C, 1576–D;* lagoon on campus UCSB, *Tanowitz & Varney 1583;* slough E of Los Carneros and Hollister Rds, *Tanowitz & Zalin 1725–A.*

H. ramosissima Benth; $n = 12$.

Road cut off Hwy 101 at Gaviota, *465–1C, 1218;* San Antonio Creek Trail near San Marcos Pass Bridge, *747, 1523;* Modoc Rd. at entrance to La Cumbre Country Club, *1525;* 0.4 mi W of Bailard Av. on Carpenteria Av., *1532-A, 1532–H;* along Arroyo Paredo Creek intersecting Hwy. 192, *1534–B;* field S of Storke and Hollister Rds., *1537–A, 1537–B, 1537–C, 1537–D, 1537–M;* El Cielito Rd. and Stanwood Dr., 0.2 mi from Sheffield Reservoir, *Tanowitz & Cowan 1589;* W side of campus lagoon, *1507;* along Casitas Pass Rd., at intersection with Livingston Canyon Rd., *2428.*

H. australis × *H. ramosissima;* $2n = 23$.

W side of campus lagoon, UCSB *1299;* field on UCSB campus near Pardall Rd., *Tanowitz & Smith 1300–E;* field E of Storke and Hollister Rds., *Tanowitz & Zalin 1517;* W side of campus lagoon UCSB, *1524*; field E of Storke and Hollister Rds., near University Village, *1538;* field near ocean bluff and San Rafael Dormitory, UCSB campus, *1568.*

TABLE 3. FREQUENCIES AND MEANS OF SYNAPTIC CONFIGURATIONS IN POLLEN MOTHER CELLS (PMC) OF HEMIZONIA AUSTRALIS × H. RAMOSISSIMA. Data derived from diakinesis or first metaphase in 155 PMC's from 4 plants.

Type	Frequency/PMC												Mean/cell
	0	1	2	3	4	5	6	7	8	9	10	11	
I	11	13	25	33	28	22	12	6	3	1	—	1	3.49
II	—	2	4	10	28	36	35	25	9	6	—	—	5.47
III	12	50	61	25	7	—	—	—	—	—	—	—	1.77
IV	74	69	11	1	—	—	—	—	—	—	—	—	0.61
V	136	19	—	—	—	—	—	—	—	—	—	—	0.12
VI	149	6	—	—	—	—	—	—	—	—	—	—	0.04

Chiasma frequency is low (approximately 14 per cell) but all chiasmata appear to terminalize fully. Most bivalents had only one chiasma. The model frequency of ring bivalents was only two per cell. Only three bivalents in all the cells analyzed contained three chiasmata. All forked trivalents had three chiasmata, while chains of three contained only two. All but four quadrivalents had three chiasmata. Pentavalents had four; hexavalents, five. Very few cells contained fragments at metaphase.

Forty-eight anaphase cells were analyzed. In every instance laggards were observed. Occasionally, univalents were left on the metaphase plate (Fig. 3) or there was precocious separation of univalents (Fig. 4). There was a very low frequency of bridges or fragments evident at this stage. Two cells had a large amount of fragmentation, giving them an appearance of being "shattered". Such spontaneous breakage has been

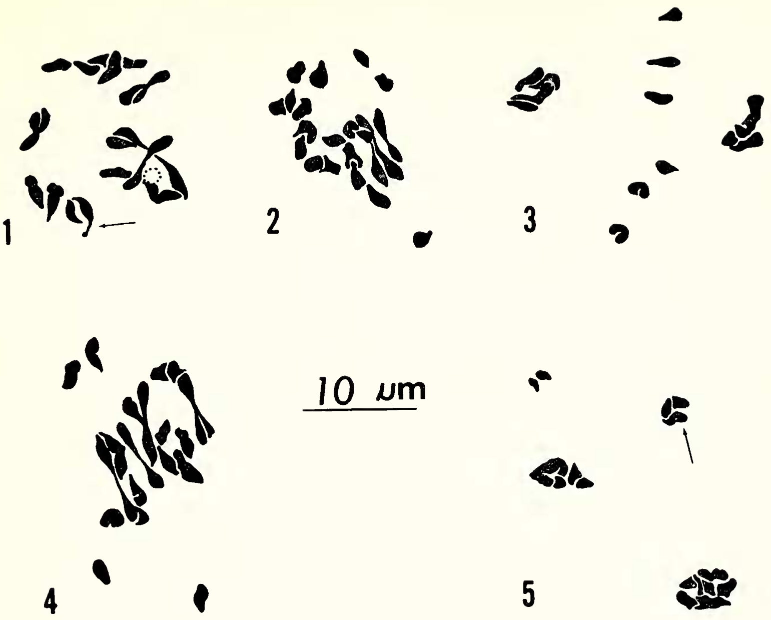

FIG. 1–5. Camera lucida drawings of meiotic chromosomes of *Hemizonia australis* × *H. ramosissima*. 1. Late diakinesis; note forked trivalents and heteromorphic pair (arrow), $2_{I} + 6_{II} + 3_{III}$; *Tanowitz 1568–B*. 2. metaphase I; univalents scattered throughout cell; *Tanowitz 1538–A*. 3. Telophase I; univalents remaining on the metaphase plate; *Tanowitz 1568–B*. 4. Early anaphase I; note precocious separation of univalents $4_{I} + 4_{II} + 2_{III} + 1_{V}$; *Tanowitz 1524–F*. 5. Telophase I with two micronuclei; note association of 3 chromosomes (arrow); *Tanowitz 1529–B*.

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described in a number of other plants (Darlington and Upcott, 1941; Walters, 1956; Burns and Gerstel, 1969). The fragments appeared to be paired and of more or less equal size.

First telophase exhibited lagging chromosomes and micronuclei. There often appeared to be an association of three chromosomes forming a micronucleus at this stage (Fig. 5). Bridge-fragment formation was as infrequent in the second division as it was in the first. Sporads of these hybrids display a great deal of variation. The range was from four to eight cells, with an average of six cells per sporad. The number of microspores per sporad ranged from one to five, with an average of three per sporad. Pollen stainability was quite low, averaging 7.2% and ranging from 0.4 to 17.2%.

Discussion

Generic sections are constructed in order either to reflect the distinctiveness between any two or more species groups or to indicate the affiliation of a group of species. Sections are generally circumscribed on the basis of morphological characters, although cytogenetic, chemical, geographical, or ecological characters are sometimes used. Sections of *Hemizonia* are morphologically circumscribed and there are numerous striking character differences between the sections. Yet earlier investigations (Clausen, 1951; Venkatesh, 1958) suggested a lower degree of divergence when the genomic make-up of the species belonging to sections *Centromadia* and *'Deinandra'* was compared.

Although the frequency of hybridization in *Hemizonia* appears to be low, it may have been more common in the earlier stages of divergence of the genus. Venkatesh (1958) suggested that the aneuploid series in sect. *Centromadia* ($n = 9, 11, 12, 13$; Johansen, 1936; Venkatesh, 1958; Table 2) may have resulted from crosses between species with disparate chromosome numbers, possibly of different sections. It is also possible that the series in sect. *'Deinandra'* ($n = 9, 10, 11, 12, 13$; Johansen, 1936; Table 2) may have resulted in this manner. Intra- as well as intersectional hybrids appear reasonable sources for speciation. Hybrids of intra- and intersectional origin were suggested for the origin of some *Clarkia* species (Lewis and Roberts, 1956). Nevertheless, intersectional hybridization in *Hemizonia* does not appear to be widespread now.

Species may have significant barriers to gene exchange maintained by both pre- and postmating isolating mechanisms (see Levin, 1971). Observations in the field suggest that both kinds of barriers occur between *H. australis* and *H. ramosissima*. Weak seasonal isolation is maintained throughout the respective ranges. *Hemizonia ramosissima* blooms earlier than *H. australis;* however, the period of overlap is significant. Microhabitat differences are found: *H. australis* occupies more saline regions than *H. ramosissima* and the hybrids are found in the intermediate areas. Pollinator constancy is quite strong where the species are in close contact (Tanowitz, ined.). Hybrid sterility is certainly evident from the data. Chromosomal differences are demonstrated clearly by the meiotic configurations in the hybrids (Figs. 1–5, Table 3) exhibiting univalents and multivalents, heteromorphic bivalents, and occasional bridges and fragments. Presumably, these meiotic irregularities contribute greatly to the sterility of the hybrids and reflect the occurrence of translocations, paracentric inversions, and perhaps other chromosomal reorganizations. None of these chromosomal differences per se necessarily preclude crossing between the species and thus many more hybrid individuals might be expected to occur; however, it is presumed that reproductive barriers, about which nothing is now known, must occur in combination with chromosomal disparity, since there is a paucity of hybrids in the field.

The hybrid plants are highly sterile annuals and obligate outcrossers (Keck, 1959; Tanowitz, ined.; Kyhos, pers. comm.). There is no evidence of introgression; only putative F_1's have been found in the sympatric populations. This suggests that gene flow is non-existent or rare and that these sharply distinctive species seemingly maintain their integrity completely. The morphological and cytogenetical evidence supports their assignment to separate sections.

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